Pulsed call sequences as contact calls in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*)

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Pacific white-sided dolphins are a group-living species and appear to exchange “contact calls” to maintain group cohesion. The aim of this study was to find and characterize their contact calls. Calls were recorded from two females at Osaka Aquarium KAIYUKAN (OAK) and three females at Izu-Mito Sea Paradise (IMSP). Because they often produced pulsed calls consecutively, a “pulsed call sequence” was defined as three or more successive pulsed calls occurring within 325 ms, which was calculated using a bout analysis. The pulsed call sequences increased during separation periods and decreased during reunions and were used for vocal exchange, suggesting that the sequences are contact calls in Pacific white-sided dolphins. Most of the pulsed call sequences were classified into unique types; several stereotyped, repeated patterns were found. One sequence type was found at OAK and the two dolphins shared the type; they exchanged sequences with type matching. On the other hand, three sequence types were found in IMSP and the three dolphins shared all of the types; however, each dolphin preferentially used different types and frequently exchanged with their own favorite types but not with type matching. These results suggest that the sequence type may function as an individual and/or group identity.

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I. INTRODUCTION

“Contact calls” may contain information regarding the identity of the caller and help mobile group-living animals maintain group cohesion and coordination (Marler, 2004; Kondo and Watanabe, 2009). When individuals are not in close physical proximity to each other but are within the effective range of acoustic signals, they can keep in touch with conspecifics by exchanging contact calls, without altering any other movement (Tyack, 2000). Various species of birds and terrestrial mammals, such as primates, elephants, and bats, use contact calls, especially while individuals are isolated/separated from conspecifics (Kondo and Watanabe, 2009). A temporal rule is found in the occurrence of contact calls; an individual responds to a call given by another within a certain period of time, which is evidence of a vocal exchange (e.g., Japanese macaques, *Macaca fuscata*: Sugiura, 1993; African elephants, *Loxodonta africana*: Soltis *et al.*, 2005; white-winged vampire bats, *Diaemus youngi*: Carter *et al.*, 2008; and large-billed crows, *Corvus macrorhynchos*: Kondo *et al.*, 2010). The identity information embedded in contact calls is correlated with social settings (Tyack, 2000). Individual identity information is essential for species that form strong inter-individual associations in flexible groupings, such as fluid fission-fusion groupings, to recognize specific individuals within their social networks (e.g., chimpanzees, *Pan troglodytes*: Mitani *et al.*, 1996; orange-fronted conures, *Aratinga canicularis*: Cortopassi and Bradbury 2000; and spider monkeys, *Ateles geoffroyi*: Ramos-Fernández, 2005). On the other hand, group identity information is more important than individual identity information for species that form stable groups; group identity allows them to easily recognize members from their own group, as well as from other groups (e.g., black-capped chickadees, *Parus atricapillus*: Nowicki, 1983; budgerigars, *Melopsittacus undulatus*: Brown *et al.*, 1988; greater spear-nosed bats, *Phyllostomus hastatus*: Boughman, 1997).

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In the ocean environment, visibility is restricted to a short range in shallow water, and the acoustic channel is advantageous for the rapid transmission of information over distance; it has led odontocetes to evolve vocal and auditory specializations for communication and echolocation (Tyack and Miller, 2002) and several odontocete species also use contact calls. As in terrestrial animals, isolated/separated situation from conspecifics elicited many contact calls from bottlenose dolphins, *Tursiops truncatus* (Caldwell *et al.*, 1990; Sayigh *et al.*, 1990; Smolker *et al.*, 1993; Janik *et al.*, 1994; Janik and Slater, 1998; Watwood *et al.*, 2005); belugas, *Delphinapterus leucas* (van Parijs *et al.*, 2003; Vergara *et al.*, 2010; Mishima *et al.*, 2015); and killer whales, *Orcinus orca* (Ford, 1989; Miller *et al.*, 2004). A particular temporal window as evidence of vocal exchanges was also found in occurrences of contact calls by bottlenose dolphins (Janik, 2000; Nakahara and Miyazaki, 2011; King *et al.*, 2013, 2014), belugas (Vergara *et al.*, 2010; Morisaka *et al.*, 2013; Mishima *et al.*, 2018), and sperm whales, *Physeter macrocephalus* (Schulz *et al.*, 2008).

Additionally, previous studies of odontocete contact calls have shown that the call types selected for contact calls and the form of identity information are species specific (e.g., Ford, 1991; Rendell and Whitehead, 2003; Janik *et al.*, 2006; Mishima *et al.*, 2018). Odontocete calls are traditionally classified into two acoustic categories: whistles and pulsed calls. Whistles are narrowband low-frequency signals with a relatively long duration (Thomson and Richardson, 1995). Pulsed calls comprise a series of several broadband pulses and are further divided into burst pulses and clicks primarily based on inter-pulse intervals (IPIs); burst pulses have shorter spaced pulses than clicks (Lammers *et al.*, 2004). In addition, several species produce mixed calls or graded calls with pulsed and tonal components (Murray *et al.*, 1998; van Parijs *et al.*, 2003; Shapiro, 2006; Tyson *et al.*, 2007; Nemiroff and Whitehead, 2009; Vergara *et al.*, 2010; Sayigh *et al.*, 2013; Kaplan *et al.*, 2014; Mishima *et al.*, 2015, 2018).

The most famous contact call in odontocetes is the signature whistle of the bottlenose dolphin (Caldwell and Caldwell, 1965; Caldwell *et al.*, 1990). Individual information is encoded in the frequency modulation patterns of the signature whistles and dolphins use these patterns independently of voice features for individual recognition (Janik *et al.*, 2006; Sayigh *et al.*, 2017). Basically, bottlenose dolphins exchange their own signatures. However, they infrequently produce copies of signature whistles (Tyack, 1986; Janik and Slater, 1998; Janik, 2000; Watwood *et al.*, 2005; Nakahara and Miyazaki, 2011; King *et al.*, 2013) of closely associated conspecifics (King *et al.*, 2013) and the copied dolphins respond to the copies by matching, namely, by calling back with their own signature whistles (King and Janik, 2013). Further, copying can also occur to match the preceding conspecifics' signature whistles (King *et al.*, 2013) and the matching (copying) elicits a response from the matched (copied) dolphin by returning the match, namely, the initiator produces its own signature whistle again (King *et al.*, 2014). Copying therefore appears to be used to address a particular individual receiver. The sophisticated individual recognition system appears to have evolved with their complex society (Janik and Sayigh, 2013). Bottlenose dolphins have a fluid fission-fusion social structure, in which group composition often changes on a daily or hourly basis, and they form core associations with particular conspecifics in their extensive social networks (Connor *et al.*, 2000). Signature whistles have been reported in the Indo-Pacific bottlenose dolphin, *T. aduncus* (Gridley *et al.*, 2014); short-beaked common dolphin, *Delphinus delphis* (Caldwell and Caldwell, 1968); Atlantic spotted dolphin, *Stenella frontalis* (Caldwell *et al.*, 1973; Herzing, 1996); Pacific humpback dolphin, *Sousa chinensis* (van Parijs and Corkeron, 2001); and Guiana dolphin, *Sotalia guianensis* (de Figueiredo and Simão, 2009; Lima and Le Pendu, 2014). However, the signature whistles in these species have only been reported to have individual distinctiveness, and no research has been conducted on these "individually distinctive" whistles having similar functions to "signature" whistles in bottlenose dolphins.

In contrast, several other odontocete species select pulsed calls or mixed calls of pulsed and tonal components for contact calls, and primarily use the temporal pattern, i.e., rhythm, of the pulse trains as the information media. Beluga whales exhibit a fission-fusion grouping pattern, although the individual relationships within groups are not well known (Bel'kovitch and Sh'ekotov, 1993; Michaud, 2005; Colbeck *et al.*, 2012). They use a burst pulse with or without a tonal component, termed "creaking calls," as their contact call, and the pulse repetition pattern appears to carry individual information because it is unique to individuals (Morisaka *et al.*, 2013; Mishima *et al.*, 2015, 2018). Copying of the creaking calls from conspecifics, as seen in bottlenose dolphins, has not been found in belugas, and they exclusively exchange their own calls. Pulsed or mixed calls similar to creaking calls may serve as individually distinctive contact calls in the closest relative to the beluga, the narwhal, *Monodon monoceros* (Ford and Fisher, 1978; Shapiro, 2006; Marcoux *et al.*, 2012). On the other hand, killer whales and sperm whales use the temporal patterns of their pulsed or mixed calls mainly for group information. Killer whales form stable matrilineal "units" and closely related units, which associate regularly with each other and are termed "pods" (Baird, 2000). They have contact calls of burst pulses with or without a tonal component called "discrete calls." Each type of discrete call has a unique pulse repetition pattern, and several types are shared within a pod (Ford, 1989, 1991), although unit-specific call types have also been observed (Miller and Bain, 2000; Weiß *et al.*, 2006). Moreover, one or more pods share parts of their call repertoires and the subsets of acoustically related pods are called acoustic "clans" (Ford, 1991; Yurk *et al.*, 2002). Some degrees of individual and unit differences exist in the acoustic structures of call types (Miller and Bain, 2000; Nousek *et al.*, 2006; Kremers *et al.*, 2012). Call type matching in vocal exchange has been found within units (Miller *et al.*, 2004). Similarly, stable matrilineal units are the basis of the social structure of sperm whales, and units temporarily form groups with one or more other units (Whitehead and Weilgart, 2000). The contact calls of sperm whales are called "codas." Codas are composed of several clicks and can be classified into distinct types based on the click repetition patterns and number of clicks (Watkins and Schevill, 1977; Weilgart and Whitehead, 1997). Several coda types are shared within a unit (Rendell and Whitehead, 2004; Schulz *et al.*, 2011). In addition, units forming a group have similar coda repertoires and the subsets of units sharing coda types are termed acoustic clans (Rendell and Whitehead, 2003). There is a ubiquitous coda type dedicated to individual identity coding (Antunes *et al.*, 2011; Gero *et al.*, 2016; Oliveira *et al.*, 2016). Coda type functioning markers of units and clans also exist (Gero *et al.*, 2016). A matching exchange of several coda types has been found among unit members (Schulz *et al.*, 2008). These findings suggest that killer whales and sperm whales may discriminate the various levels of their hierarchical social structure via their call repertoires (Gero *et al.*, 2016).

Compared with the above well-studied species, little is known about the contact calls of other odontocete species. The Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, is one of the most unstudied species in terms of acoustic communication. Pacific white-sided dolphins are distributed throughout the cold temperate North Pacific waters between latitudes 37° N and 47° N (Hobbs and Jones, 1993; Miyashita, 1993; Kanaji *et al.*, 2014). Pacific white-sided dolphins are often observed in groups of several tens; however, the group size can range from one to several thousand (Leatherwood *et al.*, 1982, 1984; Stacey and Baird, 1991; Miyashita, 1993; Black, 1994; Oswald *et al.*, 2008; Henderson *et al.*, 2011) depending on ecological and behavioral conditions (Black, 1994; Henderson *et al.*, 2011). Black (1994) reported that two Pacific white-sided dolphins that had been radio-tagged from the same group remained together during the daytime and through the late night; however, they separated during the early morning and joined up again later in the day. Given these characteristics, their society appears to have a fluid fission-fusion dynamic. Additionally, long-term associations possibly exist in their social network because a pair of dolphins within the same subgroup was resighted together after a year (Black, 1994). More information is required to gain insight into their social structure; however, if they have long-term associations in flexible groupings, we can predict that they have contact calls that encode strongly recognizable individual information, as seen in bottlenose dolphins and belugas. Pacific white-sided dolphins produce whistles (Caldwell and Caldwell, 1971; Whitten and Thomas, 2001; Oswald *et al.*, 2008); however, most of their sounds appear to be burst pulses and clicks (Oswald *et al.*, 2008). Caldwell and Caldwell (1971) showed that the whistles of captive Pacific white-sided dolphins were not individually stereotyped, which was supported by Whitten and Thomas (2001). Conversely, Caldwell and Caldwell (1967) suggested that the burst pulse function was their individually specific call. One type of burst pulse, "tin horn," was produced by two captive adult females when they were excited by any strong stimulus. The tin horns were measured at several hundred milliseconds in duration, as low frequency sounds, and were commonly produced as a couplet. The acoustic features were stereotyped intra-individually and contained constant, inter-individual differences. Thus, the tin horns functioned as individually distinctive calls; however, the small sample size utilized in this study could not prove this (Caldwell and Caldwell, 1967).

Henderson *et al.* (2011) investigated the relationship between the behavior and calls of Pacific white-sided dolphins in the Southern California Bight. During mixed contexts of foraging and milling or traveling, the dolphins produced pulsed calls and pulsed call series, which occurred in repeated patterns of at least two burst pulses. Henderson *et al.* (2011) hypothesized that the mixed contexts might indicate search behavior and/or a transition between behaviors; dolphins might use the pulsed calls and pulsed call series to communicate to each other during looking for prey, coordinating movement, and/or beginning or ending a foraging bout.

The individual distinctiveness of tin horns (Caldwell and Caldwell, 1967) and the potential communicative function of clicks, burst pulses, and burst pulse series suggested in Henderson *et al.* (2011) imply that these calls may function as contact calls for Pacific white-sided dolphins. The objective of the present study was to describe the contact call of Pacific white-sided dolphins. First, the kind of call used as a contact call was determined. Second, contact calls were categorized by type as being closest to one of the following groups: (i) bottlenose dolphin and beluga type: possess an individually-specific call type and exchange their own call type, although the copying of a conspecifics' type may infrequently occur to address a particular individual; (ii) killer whale and sperm whale type: possess a group-specific call repertoire and often exchange with type matching; or (iii) neither of these two groups. For the first step, we investigated the frequently produced calls in isolated/separated contexts and whether the occurrence of the calls was regulated by a temporal rule as evidence of a vocal exchange. For the second step, we classified contact calls into several types and examined whether each dolphin had a single type or repertoire of contact calls and whether the single type or repertoire was individually specific or shared among group members. If call types were shared, several acoustic parameters of each call type were also compared among dolphins. Further, it was investigated whether the dolphins exchanged with their own call type or with type matching.

II. METHODS

A. Subjects

Data were collected from captive Pacific white-sided dolphins at Osaka Aquarium KAIYUKAN (OAK) in Osaka, Japan from June to July 2014 and at Izu-Mito Sea Paradise (IMSP) in Shizuoka, Japan from April to June 2016. The OAK subjects were two females: K1 and K2. K1 was rescued after she strayed into a fishing net in the coastal water of Noto Peninsula in Ishikawa, Japan and came to OAK in 2009. She was estimated to be 6 years old. K2 was born from non-subject dolphins at OAK in July 2010 and was approximately 4 years old. The IMSP subjects were three females:

I1, I2, and I3. They were rescued when caught by a fixed net in the coastal waters of Noto Peninsula and came to IMSP in May 2010. It was unclear whether the three dolphins belonged to the same or different wild groups. I2 and I3 were estimated to be 13 and 10 years old, respectively, and I1 was more than 13 years old.

B. Experimental pools and recording contexts

A schematic view of the experimental pools at OAK and IMSP is shown in Fig. 1. At OAK, only K1 and K2 were kept in a backyard pool (51 m^2 surface area, 2.5 m depth), in the center of which a pole stands [Fig. 1(a)]. Nine 30-min recording sessions were performed in a normal group swimming context (observation 1). Additionally, during the experimental period, there was an occasion where the subjects were removed from the pool to trade with individuals kept in another dolphin pool at OAK in July 2014. At that time, K1 was first removed and K2 remained alone for approximately 15 min in the backyard pool. To measure the separation context, a 10-min recording was made of K2 from 5 min after K1 left (observation 2). This was the first time that K1 and K2 had been separated since they arrived at the backyard pool together in January 2013.

The main pool (22 m long, 10 m wide, and 4 m deep) of IMSP was connected to a holding pool (132 m^2 surface area, 3.2 m depth) and there was a gate between the pools [Fig. 1(b)]. The holding pool was partitioned by a fishing net and the side closest to the gate housed no dolphins. First, six 30-min recording sessions were conducted in a normal group swimming context in which I1, I2, and I3 were housed together in the main pool (observation 3). During observation 3, there were two bottlenose dolphins in the holding pool, but the gate was closed. Next, to examine the change in call usage during separation and after reunion, three additional recording sessions were performed (observation 4). During observation 4, the two bottlenose dolphins were transferred to another facility and only three Pacific white-sided dolphins were housed in the experimental pool. The observation 4 sessions comprised three sections: a 15-min group swimming period before separation, a 30-min separation period, and a 15-min group swimming period after separation. First, the three dolphins were housed in the holding pool and a 15-min recording was conducted in the group swimming context. Second, one of the dolphins remained in the holding pool and the other two dolphins were transferred to the main pool. A 30-min recording was made in the separation context. Finally, the isolated dolphin was transferred to the main pool and housed together with the conspecifics again and a 15-min recording was made in the group swimming context. The gate was closed during all contexts and prevented the isolated and non-isolated dolphins from both visual and physical communication. They could communicate acoustically, although sounds were attenuated by the closed gate. The session was performed 3 times to allow each of the three dolphins to be isolated; sessions 1, 2, and 3 targeted I1, I2, and I3 for isolation, respectively. All dolphins were usually kept together in either the main or holding pools and did not become accustomed to being isolated in the holding pool. Each observation 4 session was separated by at least 3 days.

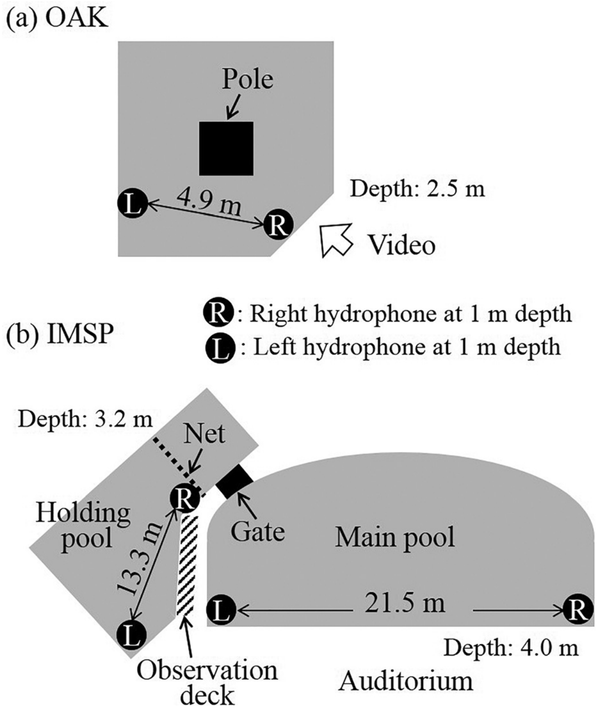


FIG. 1. Schematic view of the experimental dolphin pools at (a) OAK and (b) IMSP.

C. Recording systems and caller identification

During observations 1 and 2 at OAK, acoustic data were obtained using two TC 4013 hydrophones (Teledyne Reson, Slangerup, Denmark), with a relatively flat frequency response in the range of 1 Hz–170 kHz (-211 ± 3 dB re 1 V/μPa). The hydrophones were placed at a depth of 1 m and were separated by a distance of 4.9 m [Fig. 1(a)]. The sounds received by hydrophones were analog bandpass filtered between 1 and 200 kHz and amplified by 50 dB using an Aquafeeler III preamplifier (AquaSound, Kobe, Japan). The analog data were collected by an EZ7510 data recorder (NF, Yokohama, Japan), which digitally converted two channels of sound with 500 kHz and 16 bits sampling. Behavioral data were collected from the pool side using a GZ-V675-R video camera (JVC KENWOOD, Yokohama, Japan).

During observation 3 at IMSP, a recording system was arranged for the three Pacific white-sided dolphins in the main pool [Fig. 1(b)]. The recording system was composed of two AQH-200 hydrophones (AquaSound, Kobe, Japan), which exhibit a flat frequency response from 20 Hz to 200 kHz (over -220 dB re 1 V/μPa), an Aquafeeler III preamplifier, and an EZ7510 data recorder. The hydrophones were installed at 1 m depth and were separated by 21.5 m [Fig. 1(b)]. All settings of the preamplifier and data recorder were the same as those for observations 1 and 2, except that the gain of the preamplifier was set to 60 dB. Behavioral data were obtained from the auditorium using an HDR-CX485 video camera (Sony, Tokyo, Japan).

During observation 4, another recording system was added to collect the calls of the dolphins in the holding pool [Fig. 1(b)]. The equipment and settings were the same as those used during observations 1 and 2. The two hydrophones were installed at 1 m depth and separated by 13.3 m. The behavioral data during the group swimming in the holding pool were obtained from the observation deck in the upper side. During the separation, the behavior of only non-isolated dolphins in the main pool was recorded from the auditorium. Video recording was conducted continuously during the group swimming period in the main pool after the separation period.

Caller identification was conducted using the difference in sound arrival times between the pair of hydrophones in each pool and the position of subjects extracted from the video data. When a call was found in the data, the time difference of the call between the right and left channels was measured. The distance of the sound source from the middle line between the two hydrophones was then calculated and the side of the hyperbola was estimated. Finally, we investigated the position of all individuals in the video frame at that time, and the dolphin placed somewhere on the hyperbola was considered to be the caller. When there was an unidentified dolphin in the video frame and when more than one dolphin was placed on the calculated hyperbola, we could not determine which dolphin produced the call and the call was excluded from further analyses. During observation 3, the calls of the Pacific white-sided dolphins in the main pool could be discriminated from those of the bottlenose dolphins in the holding pool because the calls from the holding pool were barely recorded in the right hydrophone of the main pool. Similarly, during the separation period in observation 4, the calls of the isolated dolphin in the holding pool were seldom recorded in the right hydrophone of the main pool and, contrarily, the calls of the non-isolated dolphins in the main pool were seldom recorded in the left hydrophone of the holding pool. This allowed us to easily discriminate between the calls of isolated and non-isolated dolphins.

D. Call classification

One of the authors (Y.M.) classified the calls into whistles, burst pulses, and clicks based on visual and aural inspection using Audacity version 2.1.3 (The Audacity Team). Burst pulses and clicks were distinguished by IPIs; a burst pulse was a lump of pulse trains with IPIs of less than 10 ms and a click was each pulse of the pulse train with IPIs greater than 10 ms (Lammers *et al.*, 2004). Audible clicks that were often produced close to burst pulses in the time domain were analyzed; however, other almost inaudible clicks that had an energy distribution higher than 20 kHz were excluded from the analyses because these clicks appeared to be used for echolocation rather than communication (Fahner *et al.*, 2004; Nakamura and Akamatsu, 2004; Soldevilla *et al.*, 2008). The dolphins from OAK sometimes produced faint whistles that were too weak to define the start and end points. Similarly, some of their burst pulses were faint, which were clearly different from their distinct burst pulses. The faint whistles and faint burst pulses were also excluded from the analyses. Additionally, in both OAK and IMSP data, the calls of dolphins in extreme situations were not analyzed, e.g., where dolphins swam in line at very high speeds with occasional jumping.

The dolphins at both aquariums commonly produced rhythmic "pulsed call sequences" with a repeated structure of several burst pulses and clicks. To define the pulsed call sequences, we determined an appropriate cutoff time to discriminate whether pulsed calls (burst pulses and clicks) occurred independently or consecutively. The bout criterion interval of the bout analysis was used for the cutoff time (Sibly *et al.*, 1990). First, the inter-call intervals (ICIs) of the adjacent pulsed calls produced by the same individuals were measured. The ICI is defined as the time length between the end of the preceding pulsed call and the start of the following pulsed call. ICI measurements at OAK were conducted on the pulsed calls produced by K1 during observation 1 and those produced by K2 during observations 1 and 2. The ICI measurements from IMSP were conducted on the pulsed calls produced by the isolated dolphin during each session in observation 4, namely I1, I2, and I3 of sessions 1, 2, and 3, respectively. The log frequency distribution of their ICIs was constructed and fitted by the two-process exponential model to divide the distribution into the first part and the remainder, that is, intervals within bouts and intervals outside bouts (Sibly *et al.*, 1990). The bout criterion interval was calculated using the formula to minimize the total number of events that were misassigned (Slater and Lester, 1982). The statistical analysis was performed using R software version 3.1.0 (The R Foundation for Statistical Computing).

E. Analysis of the temporal production pattern of pulsed call sequences

Vocal exchange follows a temporal rule, i.e., responders call back within a particular time window and the initial callers remain silent and wait for responses in the time window. If the initial callers do not receive responses in the time window, they may produce calls again. Thus, there is a time lag between the peaks of frequency distributions of within-individual intervals (WIIs) and between-individual intervals (BIIs) of contact call production (Schulz *et al.*, 2008; Nakahara and Miyazaki, 2011; Morisaka *et al.*, 2013; Mishima *et al.*, 2018). Because the Pacific white-sided dolphins at both aquariums were likely to produce the pulsed call sequences adjacently and alternately, we anticipated that the pulsed call sequences were exchanged among the dolphins. To ascertain the prediction, WIIs and BIIs were measured at each aquarium and their frequency distributions were constructed. The time length between the end of the preceding pulsed call sequence and the start of the following pulsed call sequence was used for the interval measurements. We investigated not only whether there was a time lag between the peaks of the WII and BII distributions, but also whether the WII and BII distributions were consistent between the group swimming and separation contexts in a two-sample Kolmogorov–Smirnov test using R software.

Further, the rotation randomization techniques described in Miller *et al.* (2004) and Schulz *et al.* (2008) were performed to test whether the BII distributions were the result of vocal interaction or independent and parallel production by different dolphins using MATLAB (The MathWorks, Natick, MA). The group swimming data, observation 1 for OAK and observation 3 for IMSP, were used for the randomization test. Under the null hypothesis that each dolphin produced pulsed call sequences independently irrespective of the production of conspecifics, the start and end of each recording was linked, and the arrangement of pulsed call sequences produced by each dolphin was rotated a random amount of times with the WIIs remaining fixed. When the observed BII distributions had a peak less than a particular time, the number of BIIs within the time was tallied and the value was compared with the result of 10 000 randomizations.

F. Structure analysis of pulsed call sequences

Most of the pulsed call sequences were classified into unique types with stereotyped, repeated patterns of several kinds of pulsed calls. To describe the transition structure of each sequence type and assess their stereotypy, the syntactical analysis, which has been used for bird songs, was introduced (Okanoya and Yamaguchi, 1997). The pulsed calls constituted pulsed call sequences, termed "elements," which were classified into two to four distinct categories for each sequence type. Each of the element categories was labeled alphabetically to express a pulsed call sequence as an alphabet string and the transitions of the letters in the string were investigated. For all samples of a sequence type, the total number of occurrences was counted for each transition pattern, such as "a–a" (self-transition) and "a–b," and the transition probabilities were calculated by the total number of occurrences of each transition pattern following a particular letter divided by those of all transition patterns following the alphabet. The transition probability of each transition pattern was summarized in a matrix. The matrix also contained the probability that each element category was used for the start and end of a sequence. Based on the matrix, a transition diagram was drawn, which visually showed the transition structure and degree of sequence stereotypy of the sequence type. In the transition diagram, a set of alphabets constituting a sequence type, "start," and "end" was arranged and transitions between them expressed by arrows. The thickness of arrows was involved in the degree of transition probabilities.

The stereotypy between the element categories of a sequence type was quantified using the sequence stereotypy score in Scharff and Nottebohm (1991). Two related but different measures of sequence stereotypy, sequence linearity, and consistency, were used for the calculation of the sequence stereotypy score: $S_{\text{stereotypy}} = (S_{\text{linearity}} + S_{\text{consistency}})/2$, where $S_{\text{linearity}}$ was the number of element categories divided by the number of transition patterns without self-transitions, and $S_{\text{consistency}}$ was the number of typical transitions for each element category divided by the number of total transitions without self-transitions. High stereotypy yielded a $S_{\text{stereotypy}}$ value close to 1. The transition patterns with transition probabilities of less than 1% were excluded from the transition diagram and the calculation of the number of transition patterns in $S_{\text{stereotypy}}$.

G. Individual comparison of pulsed call sequences

The transition structure, duration, and number of elements of each sequence type were compared among individuals because the sequence types were shared among the individuals of each captive group. For the comparison of transition structures, the transition matrices of each sequence type were constructed for each dolphin. The Pearson correlation coefficient was calculated for the corresponding cells that were not zeros in the two transition matrices between each pair of dolphins (Okanoya and Yamaguchi, 1997). If the transition structures are similar to each other, then the correlation coefficient is close to 1. The duration and number of elements of each sequence type were compared using the Welch's two-sample *t*-test, Kruskal–Wallis test, and Steel–Dwass test with R software.

H. Randomization test for exchange pattern of pulsed call sequences

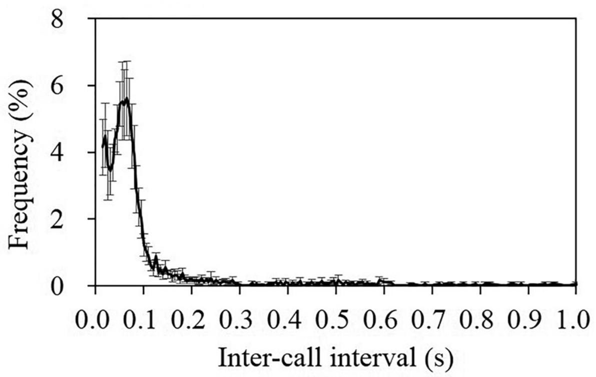
The relationship between the sequence types of callers and responders was further investigated at IMSP. Additionally, we tested whether the exchange pattern resulted from the observed data occurred more often than that expected by chance using MATLAB. A randomization test was performed under the null hypothesis that the dolphins exchanged pulsed call sequences with randomly selected sequence types from their sequence repertoire, which was constructed by pooling the number of each sequence type in all IMSP recordings for each individual. In the randomization test, the order of calling individuals within a succession of vocal exchanges remained fixed; however, the sequence types of the calling individuals were randomly selected from their data pools of pulsed call sequences without replacement. The relationship between sequence types of callers and responders of adjacent two pulsed call sequences of the randomized data was investigated. This procedure was implemented 10 000 times, and the observed exchange pattern was compared to the randomization results.

III. RESULTS

A. Classification of pulsed calls

A pulsed call sequence was defined as a succession of three or more pulsed calls with ICIs of less than 325 ms, and pulsed calls were classified into single pulsed calls, coupled pulsed calls, and pulsed call sequences. The ICIs of the adjacent pulsed calls produced by the same individuals were measured to define the pulsed call sequences. The total ICI for the samples was 5421: 1543 for K1, 879 for K2, 2230 for I1, 385 for I2, and 384 for I3. Figure 2(a) shows the frequency distribution of the mean number of ICI samples [± standard error (SE)] in percentages from the five dolphins. The number of intervals from >10 to 200 ms explained 81% of the data. The frequency distribution on a logarithmic scale showed that the pulsed calls were produced in bouts because the first part of the distribution was differentiated from the rest, i.e., the first part is intervals within bouts and the remainder is intervals outside bouts [Fig. 2(b)]. The distribution was fitted by a two-process exponential model and the bout criterion interval was calculated as

(a) Frequency (%)



(b) Log frequency

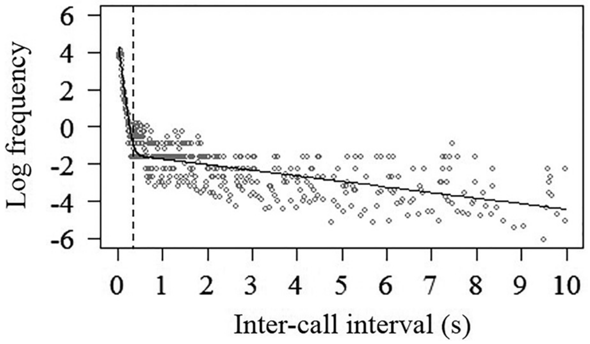


FIG. 2. Frequency distributions of intervals between adjacent pulsed calls produced by the same dolphins (a) Mean frequency (±SE) in terms of percentage from five subjects (K1: $N = 1543$; K2: $N = 879$; I1: $N = 2230$; I2: $N = 385$; I3: $N = 384$). (b) The log frequency of the intervals shows that the distribution is separated into the first part and the remainder: intervals within bouts and those outside bouts. The solid curve is the predicted two-process model. The bout criterion interval was calculated at the broken line as 325 ms. The x axis is limited to 1 s in (a) and 10 s in (b), but the distribution extended up to 15.6 min. The bin width is 5 ms.

325 ms. According to the criterion, the pulsed calls were divided into 2149 bouts. Coupled pulsed calls rarely occurred ($N = 25$) compared to single pulsed calls ($N = 1063$), tripled pulsed calls ($N = 113$), and other multiple pulsed calls ($N = 948$). Thus, we classified pulsed calls into three categories: single pulsed calls, coupled pulsed calls, and pulsed call sequences (including tripled pulsed calls and other multiple pulsed calls) (Fig. 3).

B. Single/coupled pulsed calls

A total of 32 single pulsed calls and three coupled pulsed calls were measured in the OAK recordings. The single pulsed calls had various acoustic characteristics with duration of 0.205 ± 0.528 [mean ± standard deviation (SD)] s, whereas the coupled pulsed calls were similar with duration of 0.162 ± 0.051 s. A total of 1031 single pulsed calls and 22 coupled pulsed calls were collected from the IMSP recordings. The single pulsed calls had similar characteristics, i.e., relatively low frequency, low amplitude, and short duration of 0.049 ± 0.026 s as seen in Fig. 3. Each pulsed call that was composed of the coupled pulsed calls was similar to the single pulsed calls and the duration of the coupled pulsed calls was 0.202 ± 0.102 s.

C. Call usage depending on context

The Pacific white-sided dolphins more frequently produced pulsed calls during separation than in a group swimming context. The number of each call type in different contexts is summarized in Table I. Throughout the experiments, almost all calls were pulsed calls, especially single pulsed calls and pulsed call sequences, and whistles were produced by only one of the IMSP dolphins, I3. Caller identification of only the pulsed call sequences was used for further analyses because a preliminary investigation of the temporal production pattern of the single pulsed calls demonstrated that they were not exchanged between the dolphins; thus, we predicted that the remaining predominant call, the pulsed call sequence, was used for vocal exchange and functioned as a contact call.

During observation 1, a 270-min recording was taken during the group swimming period, and 30 single pulsed

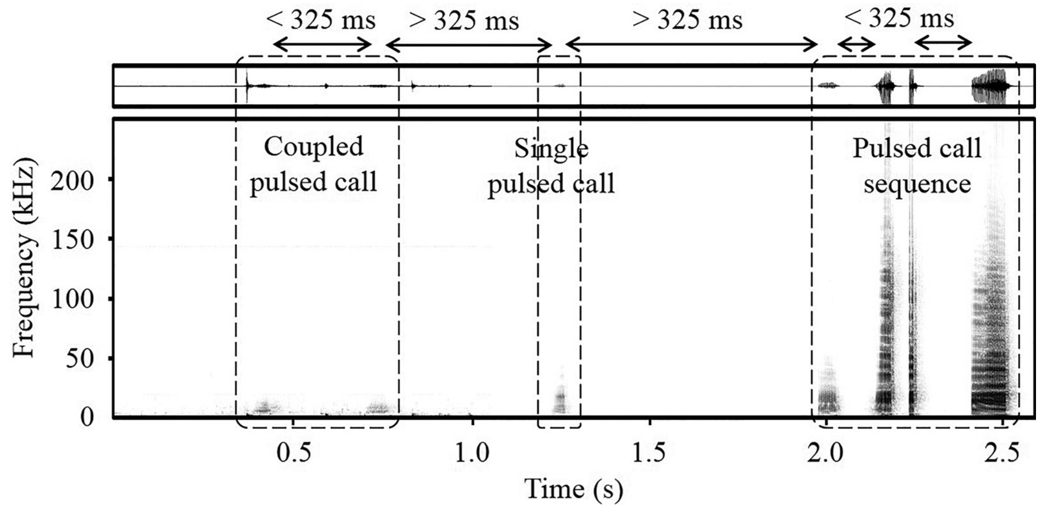


FIG. 3. Examples of single pulsed calls, coupled pulsed calls, and pulsed call sequences. A succession of three or more pulsed calls with ICIs of less than 325 ms was defined as a pulsed call sequence. The example of a pulsed call sequence was composed of four elements (Avisoft SASLab Pro version 5.2, Avisoft Bioacoustics, Germany; fast Fourier transform (FFT) size: 1024 points; window: Hamming; overlap: 50%).

TABLE I. Number of each call type in different contexts: group swimming (GS) and separation (S). The numbers of callers identified from pulsed call sequences are shown in parentheses and their details are represented below the parentheses.

Aquarium	OAK		IMSP										
Observation no.	1	2	3	4									
Session no.				1			2			3			
Context	GS	S	GS	GS	S	GS	GS	S	GS	GS	S	GS	
Recording time (min)	270	10	180	15	30	15	15	30	15	15	30	15	
Whistle	0	0	0	0	0	0	0	0	0	0	15	0	
Single pulsed call	30	2	286	0	311	22	30	180	13	0	189	0	
Coupled pulsed call	3	0	5	0	7	1	0	6	0	0	3	0	
Pulsed-call sequence	256	24	103	0	412	8	1	130	0	0	127	0	
(Caller identification)	(183)	(24)	(78)	(0)	(394)	(8)	(1)	(123)	(0)	(0)	(124)	(0)	
	K1:126		11:25		11:201	11:4		11:42			11:36		
	K2:57	K2:24	12:38		12:91	12:2		12:38			12:38		
			13:15		13:102	13:2	13:1	13:43			13:50		

calls, three coupled calls, and 256 pulsed call sequences were collected. Of the 256 pulsed call sequences, 183 had callers identified, including 126 from K1 and 57 from K2. During observation 2 of the 10-min recording for isolated K2, K2 produced two single pulsed calls and 24 pulsed call sequences for 6 min after the start of the recording, and no calls were produced after. The ratio of pulsed call sequences produced by K2 during the separation period was higher than that during the group swimming period; the ratio of pulsed call sequences in the first 6 min of the separation period was 4.0/min, while it was only 0.5 ± 0.5 (mean ± SD)/min during each 30-min session of the group swimming context, even if all callers of the unidentified pulsed call sequences were considered to be K2.

During observation 3, a 180-min recording was made during the group swimming period, and 286 single pulsed calls, five coupled pulsed calls, and 103 pulsed call sequences were collected. Observation 4 showed that the ratio of pulsed calls, particularly single pulsed calls and pulsed call sequences, increased during the separation periods and decreased during the reunions. During session 1, no single pulsed calls or pulsed call sequences were measured during the group swimming period before I1 isolation, whereas 311 single pulsed calls and 412 pulsed call sequences were obtained during I1 isolation. During the group swimming period after I1 isolation, only 22 single pulsed calls and eight pulsed call sequences were obtained. During session 2, only 30 single pulsed calls and one pulsed call sequence were collected before I2 isolation, whereas 180 single pulsed calls and 130 pulsed call sequences were collected during I2 isolation. There were only 13 single pulsed calls after I2 isolation. During session 3, there were no calls before or after I3 isolation, whereas 189 single pulsed calls and 127 pulsed call sequences were collected during I3 isolation.

D. Temporal production pattern of pulsed call sequences

A temporally regulated production pattern was found in the pulsed call sequences at both aquariums. At OAK, 73 WIIs and 72 BIIs for pulsed call sequences were collected from the group swimming data of observation 1 and only 23 WIIs were collected from the separation data of observation 2. The WII and BII frequency distributions during the group swimming period had a sharp peak at 1.0 and 0.5 s, respectively, and the WII distribution did not significantly differ from that during the separation period [Fig. 4(a)]; two-sample Kolmogorov–Smirnov test: $D = 0.253$, $P = 0.178$). From the group swimming BII samples, 23 (31.9%) occurred within 1 s and the value was significantly greater than the expected value of 1.2 ± 1.5 (mean ± SD) generated by the rotation randomizations ($P < 0.0001$).

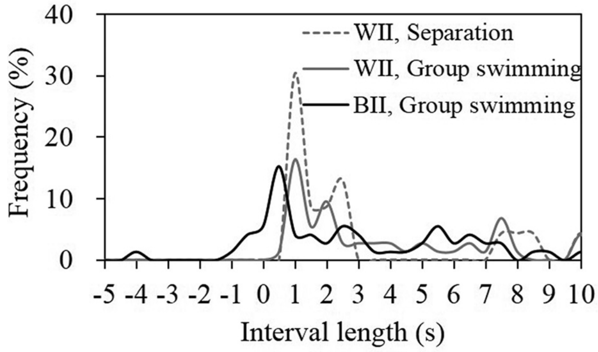
At IMSP, 69 BIIs and 10 WIIs were collected from the group swimming data of observation 3. Because of the small sample size, the frequency distribution of WIIs was not determined. From the separation data of observation 4, 149 WIIs and 487 BIIs were collected. The WII and BII frequency distributions during the separation periods had a gradual peak at 1.0–1.5 s and 0–0.5 s, respectively, and the BII distribution was not significantly different from that during the group swimming period [Fig. 4(b); two-sample Kolmogorov–Smirnov test: $D = 0.111$, $P = 0.449$]. From the group swimming BII samples, 48 (69.6%) occurred within 1.0 s and the value was significantly greater than the expected value of 1.3 ± 2.4 (mean ± SD) generated by the rotation randomizations ($P < 0.0001$).

E. Structure of pulsed call sequences

A total of 280 pulsed call sequences from OAK dolphins had similar sequence structures and were classified into a distinct type, type K (Fig. 5). However, the 781 pulsed call sequences obtained from the IMSP dolphins were classified into three unique types, type I-1 ($N = 330$), type I-2 ($N = 145$), and type I-3 ($N = 262$), and one "others" type ($N = 44$). There were mixed sequences comprising all or two of the three unique types and other sequences without distinct repetition pattern, and these were included in the others group.

The elements constituting type K were classified into three categories and labeled a, b, and c [Fig. 5(a)]. Similarly, the elements constituting type I-1, type I-2, and type I-3 were classified into four (h, i, j, k), three (p, q, r), and two

(a) OAK



(b) IMSP

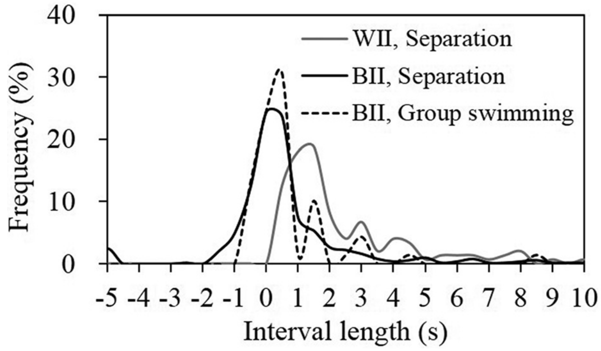


FIG. 4. Frequency distributions of WIIs and BIIs of pulsed call sequences. (a) OAK and (b) IMSP. In (a), WIIs were collected from the group swimming data from observation 1 ($N = 73$) and separation data from observation 2 ($N = 23$), but BIIs were collected only from the group swimming data ($N = 72$). In (b), BIIs were collected from both the group swimming data of observation 3 ($N = 69$) and the separation data of observation 4 ($N = 487$), but WIIs were only collected from the separation data ($N = 149$). The x axis is limited to 10 s, but the distribution extended up to 4.3 min in (a) and 19.9 min in (b). The bin width is 0.5 s.

(x, y) categories, respectively [Figs. 5(b)–5(d)]. Syntactical analyses were performed on 270 out of 280 type K samples and all of type I-1, type I-2, and type I-3 samples. From the total number of type I-1, type I-2, and type I-3, 2.4%, 4.8%, and 0.4%, respectively, began with a burst pulse that was different from the burst pulses in their element categories, i.e., had similar characteristics to the single pulsed calls. The first burst pulses in the rare cases were therefore excluded from the transition matrices and subsequent analyses. The transition diagrams showed that each of the sequence types mainly consisted of thick arrows with transition probabilities of >10% (Fig. 5). The sequence stereotypy scores were calculated as 1.00 for type K, 0.90 for type I-1, 1.00 for type I-2, and 1.00 for type I-3.

The duration of each sequence type was 0.95 ± 0.52 (mean ± SD) s for type K, 0.78 ± 0.37 s for type I-1, 0.81 ± 0.33 s for type I-2, and 1.05 ± 0.49 s for type I-3. The number of elements of each sequence type was 12.5 ± 6.9 for type K, 5.6 ± 2.2 for type I-1, 7.4 ± 2.8 for type I-2, and 11.3 ± 5.1 for type I-3.

F. Individual comparison of pulsed call sequences

The OAK dolphins shared one type of pulsed call sequence, type K. The Pearson correlation coefficient of the transition matrices for type K sequences was calculated as 1.00 between K1 and K2 during the group swimming period. However, the duration and number of elements were significantly different inter-individually (Fig. 6; Welch's two-sample t-test: $t_{166} = 3.67$, $P < 0.05$ for duration; $t_{177} = 4.20$, $P < 0.05$ for the number of elements).

The three typical types, type I-1, type I-2, and type I-3, of pulsed call sequences were produced by all IMSP dolphins. Figure 7 shows the proportion of each sequence type produced by each dolphin in different contexts: the group swimming context of observation 3 and each separation context of session 1, 2, and 3 in observation 4 (I1 isolation, I2 isolation, and I3 isolation contexts). I1, I2, and I3 mainly produced type I-1, type I-2, and type I-3, respectively, in any context. From the pulsed call sequences produced by I1, type I-1 sequences occupied 100% during the group swimming period, 47.8% in I1 isolation, 92.9% in I2 isolation, and 91.7% in I3 isolation. Similarly, of the pulsed call sequences produced by I2, type I-2 sequences occupied 47.4% in the group swimming period, 70.3% in I1 isolation, 39.5% in I2 isolation, and 52.6% in I3 isolation. From the pulsed call sequences produced by I3, type I-3 sequences occupied 66.7% during the group swimming period, 85.3% in I1 isolation, 65.1% in I2 isolation, and 60.0% in I3 isolation.

The pulsed call sequences during the separation periods were used for inter-individual comparison of each sequence type. The Pearson correlation coefficients for the transition matrices of type I-1 were 0.99 between I1 and I2, 0.95 between I1 and I3, and 0.98 between I2 and I3. Similarly, the correlation coefficients for the transition matrices of type I-2 were 0.92 between I1 and I2, 0.93 between I1 and I3, and 0.75 between I2 and I3. The correlation coefficients for the transition matrices of type I-3 were 0.74 between I1 and I2, 0.37 between I1 and I3, and 0.88 between I2 and I3. There was a significant individual difference in the duration of all sequence types (Kruskal–Wallis test: $H_2 = 45.53$, $P < 0.05$ for type I-1; $H_2 = 31.30$, $P < 0.05$ for type I-2; $H_2 = 22.97$, $P < 0.05$ for type I-3, respectively). However, a pairwise comparison of duration showed one to two pairs of individuals had no significant difference in all sequence types [Fig. 6(a); Steel–Dwass test: $\alpha = 0.05$]. Although the number of elements of each sequence type had a significant individual difference (Kruskal–Wallis test: $H_2 = 36.90$, $P < 0.05$ for type I-1; $H_2 = 44.17$, $P < 0.05$ for type I-2; $H_2 = 31.49$, $P < 0.05$ for type I-3), a pairwise comparison showed one pair of individuals had no significant difference in type I-2 and type I-3 [Fig. 6(b); Steel–Dwass test: $\alpha = 0.05$]. The duration and number of elements varied contextually rather than inter-individually in both aquariums; they were greater during the separation periods than during the group swimming periods, except for in type I-2 (see Fig. S1 in the supplementary material[1]).

G. Usage of the shared typical types of IMSP pulsed call sequences during exchanges

The IMSP dolphins shared the three typical types of pulsed call sequences; they tended to exchange pulsed call sequences with their own favorite types, but not with type

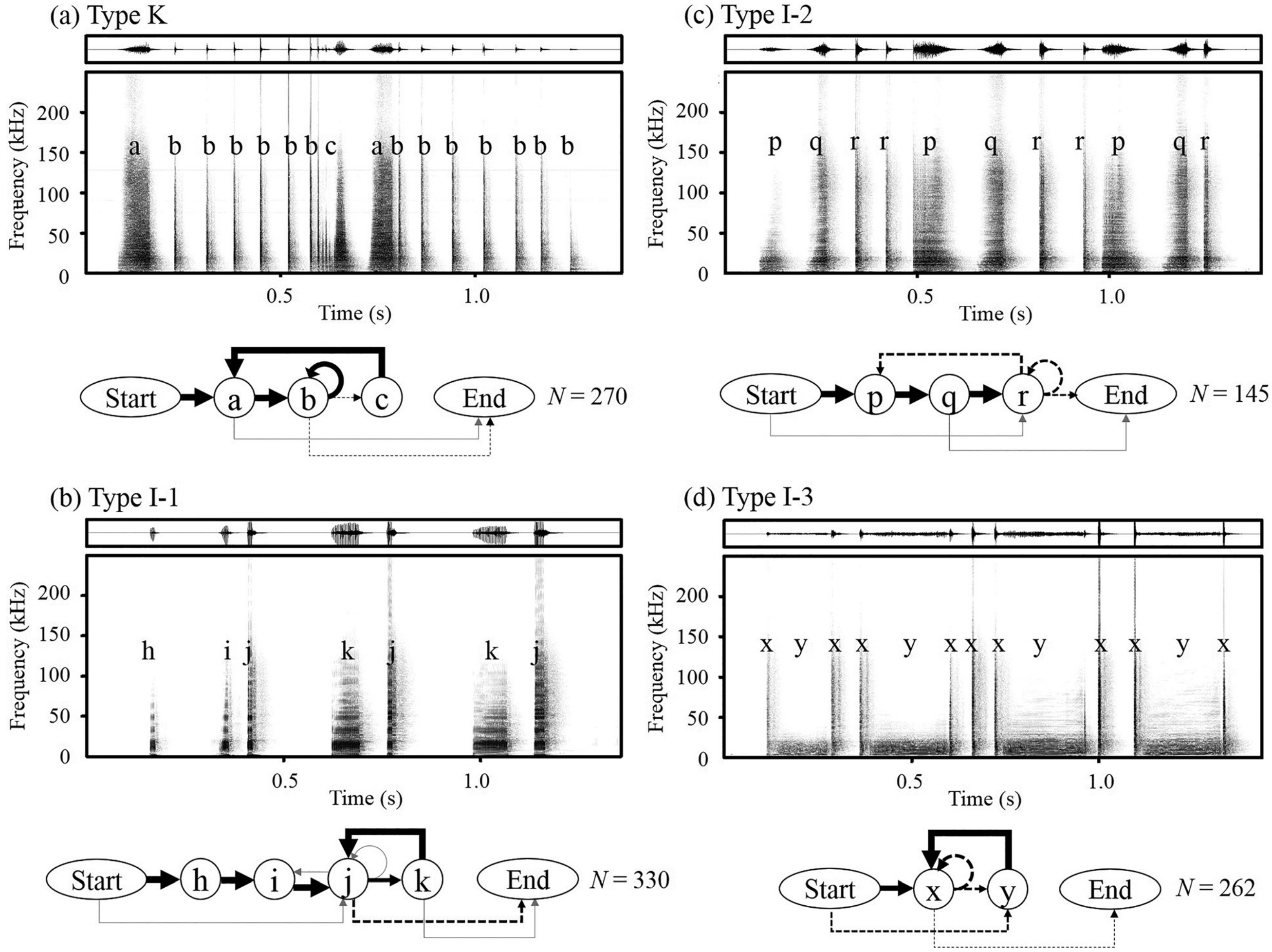


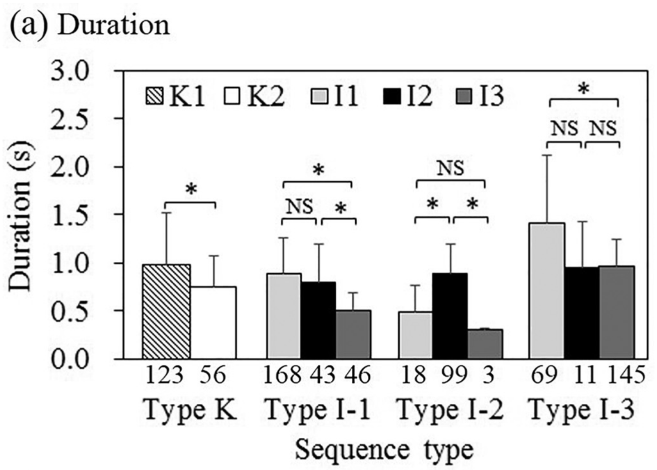
FIG. 5. Each type of pulsed call sequence: (a) type K; (b) type I-1; (c) type I-2; and (d) type I-3. The top graphs represent the examples of a waveform and spectrogram (FFT size: 1024 points; window: Hamming; overlap: 50%). The elements constituting each sequence type were classified and labeled alphabetically as shown in the spectrograms. The bottom graphs represent the transition diagrams. The black solid line, black broken line, and gray solid line indicate transition probabilities of 50%–100%, 10%–50%, and 1%–10%, respectively. The number of samples is described on the right of each transition diagram.

matching. Based on the temporal production pattern in Fig. 4, the two adjacent pulsed call sequences occurring within 1 s and produced by different dolphins were considered as vocal exchanges. First, from all data collected from IMSP dolphins, the proportion of favorite and non-favorite types of pulsed call sequences used for vocal exchange was calculated. The favorite types, type I-1 for I1, type I-2 for I2, and type I-3 for I3, produced in the process of vocal exchange accounted for 79.6%, 83.9%, and 91.7% of their total favorite type numbers, respectively. The ratio of the other two non-favorite types for each dolphin, which were produced in the vocal exchange process, was approximately 28%–100% (I1: 27.8% for type I-2 and 76.1% for type I-3; I2: 64.2% for type I-1 and 52.6% for type I-3; and I3: 60.0% for type I-1 and 100% for type I-2).

Second, the relationship between the sequence types used by the callers and responders of vocal exchanges were investigated using all data from IMSP dolphins. A total of 390 exchanges were identified, of which 354 (90.8%) were where both callers and responders used one of the typical three types of pulsed call sequences. From the 354 exchanges, 207 (58.5%) were the most frequent exchange patterns where both callers and responders produced their favorite types, 86 (24.3%) were matching exchanges of sequence types, which broke down into three matching patterns, i.e., 32 (9.0%) were that callers produced their favorite types and responders called back (matching pattern 1), 49 (13.8%) were that callers produced one of the non-favorite types and the responders who preferred the type called back (matching pattern 2), and 5 (1.4%) were that callers produced one of the non-favorite types and the responders who also did not prefer the type called back (matching pattern 3). The number of the most frequent exchange pattern that both callers and responders using their favorite types significantly exceeded the expected value of 174.9 ± 7.9 (mean ± SD) generated by randomizations ($P < 0.0001$) but not the number of matching exchanges (expected: 99.7 ± 7.9, $P = 0.97$ for all matching exchanges; 44.7 ± 5.5, $P = 0.99$ for matching pattern 1; 45.3 ± 5.5, $P = 0.29$ for matching pattern 2; 9.7 ± 2.9, $P = 0.97$ for matching pattern 3).

IV. DISCUSSION

The present study demonstrated that the contact calls of Pacific white-sided dolphins were pulsed call sequences and



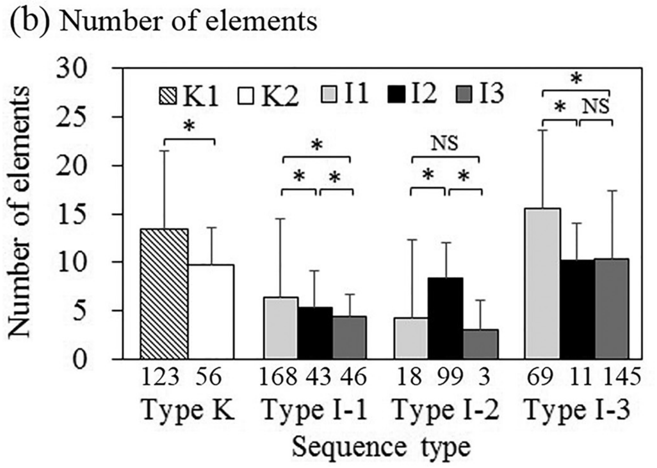
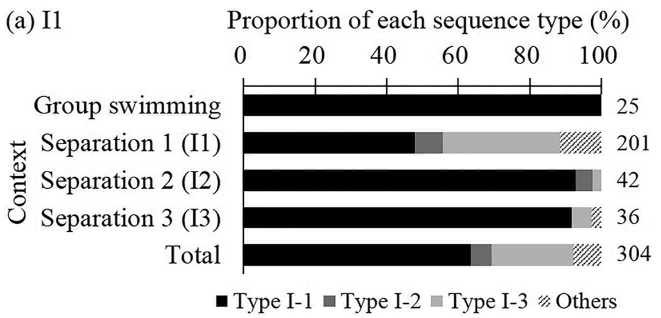
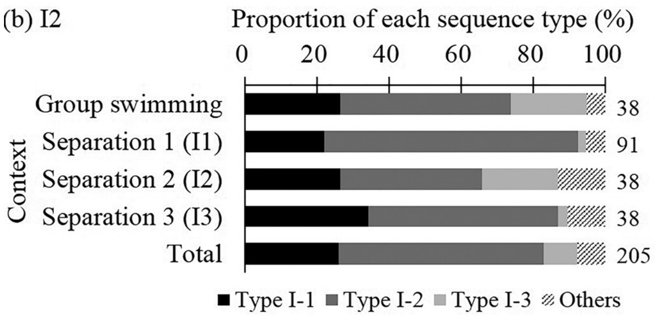


FIG. 6. Individual comparison for the (a) duration and (b) number of elements of each type of pulsed call sequence. Columns and bars represent the mean ± SD. The samples of type K were collected from the group swimming data of observation 1. The samples of type I-1, type I-2, and type I-3 were collected from the separation data of observation 4. The total number of samples is described below each column. The asterisks denote significant differences between K1 and K2 (Welch's two-sample t-test: $P < 0.05$) or among I1, I2, and I3 (Steel–Dwass test: $P < 0.05$). NS, not significant.





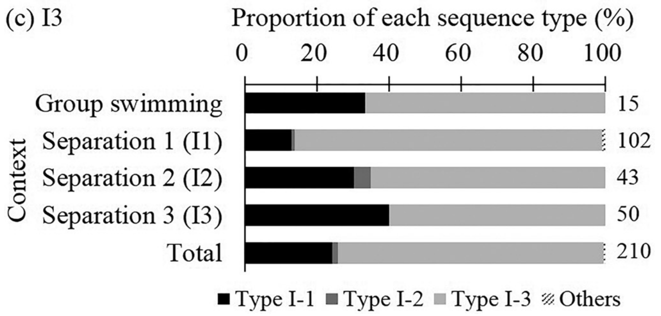


FIG. 7. Proportion of each type of pulsed call sequence for each IMSP dolphin, (a) I1, (b) I2, and (c) I3, in different contexts: the group swimming context in observation 3 and each separation context in observation 4. The isolated dolphin in each separation is shown in parentheses. The total number of pulsed call sequences in each context is described to the right of the bar.

the sequence type carried individual and/or group identity information. The two dolphins from OAK produced no whistles except for faint whistles and one out of the three dolphins from IMSP produced only 15 distinct whistles in the total recordings. Thus, Pacific white-sided dolphins include whistles in their call repertoire, as has been shown in previous studies (Caldwell and Caldwell, 1971; Whitten and Thomas, 2001); however, they mainly use pulsed calls rather than whistles for communication.

The Pacific white-sided dolphins in the present study produced pulsed calls sequentially as described by Henderson *et al.* (2011). Therefore, pulsed calls were divided into single pulsed calls, coupled pulsed calls, and pulsed call sequences (Fig. 3). K2 from OAK most commonly produced pulsed call sequences soon after separation from K1, and the production rate of pulsed call sequences during the separation period was higher than that during the group swimming period (Table I). The dolphins from IMSP produced pulsed calls more frequently during the separation periods than during the group swimming periods, especially during the first separation period of session 1 in observation 4, which elicited a lot of pulsed calls from the dolphins. The most predominant call type was the pulsed call sequence during the separation period of session 1, whereas the single pulsed call was the most common during the separation periods in sessions 2 and 3.

The pulsed call sequences were exchanged among dolphins (Fig. 4). There was a time lag between the WII and BII distributions of pulsed call sequences in both aquariums, with peaks of approximately 1.0–1.5 s and 0–0.5 s, respectively, and distributions did not vary depending on contexts. Additionally, the number of BIIs occurring within 1 s was greater than that expected by chance. These results suggest that the pulsed call sequences were used for vocal exchange following a consistent temporal rule, with responders calling back in less than approximately 1.0 s and callers remaining silent within that time. This temporal rule regulating vocal exchange is similar to that of contact calls in bottlenose dolphins (Janik, 2000; Nakahara and Miyazaki, 2011; King *et al.*, 2013, 2014) and belugas (Morisaka *et al.*, 2013; Mishima *et al.*, 2018). Given that the pulsed call sequences were commonly produced in separation contexts and exchanged among dolphins, we concluded that the pulsed call sequences were the contact calls of the Pacific white-sided dolphin. The pulsed call series in Henderson *et al.* (2011), which was produced during mixed contexts of foraging and milling or traveling, is similar to the pulsed call sequences in the present study. The mixed contexts possibly represent search behavior and/or a transition between behaviors, as suggested in Henderson *et al.* (2011), and the burst-pulse series might play a role in maintaining group cohesion and coordination in the contexts.

The two dolphins from OAK produced a single type of pulsed call sequences, type K, whereas the pulsed call sequences produced by the three dolphins from IMSP were classified mainly into three distinct types, type I-1, type I-2, and type I-3, which were shared among the dolphins (Fig. 5). Each sequence type in both aquariums was produced in a highly stereotyped manner, with a sequence stereotypy score of above 0.9. In addition, the transition structure of each sequence type appeared to be consistent among individuals because the Pearson correlation coefficients for the transition matrices of all sequence types were above 0.7 between each pair of individuals. The one exception was for type I-3, where the coefficient was 0.37 between I1 and I3. The duration and number of elements of each sequence type seemed to be flexible parameters; these parameters varied contextually rather than inter-individually. Although the parameters of type K were significantly different between K1 and K2 and those of type I-1, type I-2, and type I-3 were significantly different among I1, I2, and I3, a pairwise comparison of the dolphins from IMSP showed that these parameters were not always different between each pair of individuals (Fig. 6). On the other hand, they were significantly greater in separation contexts than in group swimming contexts, except for type I-2 (see Fig. S1 in the supplementary material[1]). Thus, these parameters might flexibly change depending on the psychological state, and coincide with those of contact calls in bottlenose dolphins and belugas, the durations of which change contextually (Esch *et al.*, 2009; Mishima *et al.*, 2018).

The pulsed call sequences of the Pacific white-sided dolphins probably belong to the group that contains neither of the two representative types of contact calls (i.e., group III), with group I (bottlenose dolphin and beluga type) possessing basically one individually specific call type and exchanging their own call type, although copying of conspecifics' type may infrequently occur to address a particular individual and group II (killer whale and sperm whale type) possessing a group-specific call repertoire and exchanging with type matching. Rather, the pulsed call sequences were characterized as intermediate contact calls between groups I and II because they partly contained the characteristics of both groups. From the social structure of Pacific white-sided dolphins, long-term associations in flexible groupings suggested by Black (1994), we could predict that they possess similar contact calls to bottlenose dolphins and belugas, but our results did not simply support it. The sharing of the stereotypes of pulsed call sequences between OAK dolphins and among IMSP dolphins suggests that Pacific white-sided dolphins share one or more group-specific sequence types within the group II members. Thus, the two OAK dolphins shared one sequence type, type K, and exchanged with type matching. There was, however, preferential use of one of the sequence types for the IMSP dolphins in not only separations but also in group swimming; type I-1 of I1, type I-2 of I2, and type I-3 of I3 accounted for approximately 40%–100% of their pulsed call sequences (Fig. 7). Moreover, the exchange pattern that both callers and responders used their own favorite types occurred most frequently (58.5%) at above chance level; however, matching exchanges of sequence types occurred less frequently (24.3%) at below chance level. The results from the IMSP dolphins imply that type I-1, type I-2, and type I-3 might function as individually distinctive types of I1, I2, and I3, respectively, and could be used for a degree of individual identity advertisement in vocal exchange as group I.

However, it was unlikely that the non-favorite types of each IMSP dolphin were produced toward an intended dolphin for addressing as seen in bottlenose dolphins (King and Janik, 2013; King *et al.*, 2013, 2014) of group I. The production rate of non-favorite types was relatively higher than that of the copying rate of conspecifics' signatures in bottlenose dolphins. The maximum proportion of a non-favorite type was 33% during the group swimming period, 40% during their own isolation period, and 34% during conspecifics' isolation periods (Fig. 7). For bottlenose dolphins, the copying of conspecifics' signatures rarely occurred in group swimming contexts or in their own isolation and conspecifics' isolation contexts (Janik and Slater, 1998; Watwood *et al.*, 2005; Nakahara and Miyazaki, 2011; King *et al.*, 2013) and the signature whistles of conspecifics occupied a minor part of the call repertoire of the copier, probably to maintain reliable identity information, although one report showed that two captive bottlenose dolphins during group swimming produced the other's signature whistles at 19% and 21% (Tyack, 1986). The addressing that is seen in bottlenose dolphins were matching patterns 1 and 2 shown in the present study. Matching pattern 1 represents matching by the second caller to the favorite types of the initial caller and matching pattern 2 represents addressing by the initial caller followed by the matching response of the addressed dolphin. Of the 354 total exchanges, the number of exchanges of matching patterns 2 and 1 were 49 and 32, which were the second and third highest values in all exchange patterns, respectively; however, the numbers of both matching patterns were not greater than that of the expected values (King and McGregor, 2016). Furthermore, approximately 80%–84% of the favorite types for each IMSP dolphin occurred during vocal exchange, whereas the percentage ranged from 28% to 100% in the non-favorite types. This relatively low percentage indicated that the non-favorite type produced by the caller was mostly used for neither initiation nor vocal exchange response.

From the two captive groups in the present study, it is difficult to understand the entire characteristics of the contact calls of Pacific white-sided dolphins. It is definite that the sharing of sequence types occurs among conspecifics irrespective of kinship. At OAK, even though the wild-born K1 and captive-born K2 were not related, they shared a sequence type. At IMSP, although the original wild group of the three dolphins was unknown, if they belonged to different wild groups, they shared three sequence types since their arrival at IMSP. However, it is not yet clear how the shared types of pulsed call sequences function. OAK dolphins produced a single sequence type, which resulted in exchange with type matching. In contrast, each of the dolphins from IMSP preferentially used different shared call types and tended to exchange with their own favorite type but not with type matching. However, the favorite type for a dolphin occupied a maximum 30%–40% of the call repertoire of other dolphins and the non-favorite types for each dolphin were not used for addressing purposes. Thus, the pulsed call sequences of Pacific white-sided dolphins partly contained characteristics of both groups I and II, and we cannot say whether the pulsed call sequences belong to group I or group II, rather we can imply that they are characterized as intermediate contact calls of groups I and II.

The investigations of relationship among the number of dolphins, repertoire size, and exchange pattern of pulsed call sequences and the effect of change of group members on their sequence repertoire are important for gaining insight into the function of sequence types. In addition, longitudinal studies of calves' calls would also allow us to understand how they develop the sequence types. Sharing of sequence types occurred regardless of kinship; therefore, it is conceivable that dolphins can obtain sequence types by production learning, which enables animals to modify their signal structure as a result of experience with those of other individuals (Janik and Slater, 2000). Further, it should be examined how the Pacific white-sided dolphins discriminate callers of the shared sequence types. The sequence structure, duration, and the number of elements did not appear to have enough inter-individual differences to discriminate each other (Fig. 6). The finer variations in timing of each element within a sequence type may be a candidate of the individual information media as seen in the pulse type contact calls of killer whales (Nousek *et al.*, 2006) and sperm whales (Antunes *et al.*, 2011; Gero *et al.*, 2016; Oliveira *et al.*, 2016). We should also advance research on the social structure of wild Pacific white-sided dolphins, as well as the usage of pulsed call sequences to understand the form of identity information embedded in them, because the identity information in contact calls is correlated with the social structure (Tyack, 2000).

The present study classified elements of pulsed call sequences into alphabetical categories spectrographically and aurally, and the elements of different sequences were allocated to different categories. However, there were similar elements among sequence types, for example "j" of type I-1, "r" of type I-2, and "x" of type I-3. As a next step, we should statistically compare the elements among different sequence types as well as within a sequence type by using acoustic parameters such as peak frequency or a change in IPIs. This would uncover the repertoire size of elements comprising pulsed call sequences.

We further asked the function of other pulsed call sequences as seen in IMSP, such as mixed sequences comprising all or some of type I-1, type I-2, and type I-3, and unstereotyped pulsed call sequences without distinct repetition pattern. Additionally, the role of the single and coupled pulsed calls should be investigated. Especially, multiple single pulsed calls, which were independently produced and were low frequency, low amplitude calls with a mean duration of 0.049 s, were collected from IMSP dolphins. The few coupled pulsed calls might be repetitions of the single pulsed calls because each burst pulse of the coupled pulsed calls were similar to the single pulsed calls. The tin horns measured in Caldwell and Caldwell (1967) were low frequency calls but were several hundred milliseconds in duration and were often produced as a couplet. Thus, the single pulsed calls appeared different to that of the tin horns, although the call definition was different between the studies, which might affect the difference. Rather, the tin horns were probably included in the pulsed call sequences.

It was still unknown why the Pacific white-sided dolphins selected pulsed call sequences as contact calls. Odontocetes obtained pulsed calls when they diverged from mysticetes, and whistles emerged in the groups after Ziphiidae (Morisaka and Connor, 2007; Morisaka, 2012). The use of whistles for contact calls seemed to emerge in several Delphinidae species, but the selective pressure is still under debate (Morisaka, 2012). The natural habitat of Pacific white-sided dolphins (Hobbs and Jones, 1993; Miyashita, 1993; Kanaji *et al.*, 2014) overlaps with the distributions of Delphinidae species that use whistle-type contact calls, such as bottlenose dolphins and short-beaked common dolphins (Mann *et al.*, 2000); the environmental factor may not lead the call-type selection. The genus *Cephalorhynchus* lost whistles and shifted the frequency range of pulsed calls to higher than 100 kHz; this is a higher frequency than their predator, killer whales, can hear (Morisaka and Connor, 2007). Pacific white-sided dolphins and Delphinidae species using whistle-type contact calls are also in danger of predation by killer whales, but the frequency range of their pulsed call sequences and whistles overlap with the audible range of killer whales. Thus, several benefits may exist that exceed the cost of predation.

The phylogenies of *Lissodelphis*, *Lagenorhynchus*, and *Cephalorhynchus* species are still under debate, but it is likely that *Lissodelphis* is closely related to *Lagenorhynchus* species, and the dusky dolphin, *Lagenorhynchus obscurus*, is the most closely related species to Pacific white-sided dolphins (LeDuc *et al.*, 1999; Pichler *et al.*, 2001; Harlin-Cognato and Honeycutt, 2006; May-Collado and Agnarsson, 2006; McGowen *et al.*, 2009; McGowen, 2011; Banguera-Hinestroza *et al.*, 2014; Lee *et al.*, 2018). Sequences of burst pulses that were similar to the pulsed call sequences of the Pacific white-sided dolphins in the present study have been found in the northern right whale dolphin, *Lissodelphis borealis*, and the dusky dolphin (Rankin *et al.*, 2007; Vaughn-Hirshorn *et al.*, 2012). Rankin *et al.* (2007) recorded calls from seven groups of northern right whale dolphins off the west coast of Oregon, California, and Washington. All of their 129 burst pulses occurred in sequence and each sequence comprised 6–18 burst-pulse elements. In the sequences, there were eight unique stereotyped types and most of the sequence types were repeatedly produced in succession. Specific sequences were detected in one group or one subgroup. Vaughn-Hirshorn *et al.* (2012) investigated the sounds of dusky dolphins from 22 feeding groups in

Admiralty Bay and Current Basin in New Zealand, and two groups engaging in resting, traveling, and socializing behavior in Golfo Nuevo in Argentina. The 42% of burst pulses in New Zealand and the 64% of burst pulses in Argentina occurred in sequence. There were 2–14 burst-pulses elements in a sequence and the elements closely matched each other aurally and in spectrograms and waveforms. There was a variety of sequence types and almost all the types were infrequently recorded except for one type that was frequently recorded at both study sites. The function of these calls in the northern right whale dolphins and dusky dolphins is still unclear, but the calls perhaps have similar communicative roles to the pulsed call sequences of the Pacific white-sided dolphins. Additionally, in the Hawaiian melon-headed whale, *Peponocephala electra*, some of the "repeated calls" that have potential as contact calls were composed of burst-pulse combinations with or without tonal components (Kaplan *et al.*, 2014). More information regarding other species is required to uncover the evolutional pathway of the pulsed call sequences.

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[1] See supplementary material at https://doi.org/10.1121/1.5116692 for the contextual comparison of the (a) duration and (b) number of elements of each type of pulsed call sequence between the group swimming and separation periods.

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